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# Changes in organic-chemical components and ingrowth of fungal mycelium in decomposing birch leaf litter as compared to pine needles

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With 6 figures

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## 1. Introduction

In many forest ecosystems litter decomposition is the major pathway for the supply of plant nutrients to the soil. As litter is an organic-chemical carrier of nutrients its decomposition is a limiting process for nutrient release. Decomposition of litter is basically carried out by microorganisms, and the rates of litter breakdown are dependent on the temperature and moisture of the litter as well as of substrate quality. The latter, reflecting the litter's chemical composition is an important regulatory factor. Some studies have related decomposition rates to the organic and inorganic-chemical composition of the litter. Thus MELIN (1928) found that the percentage of nitrogen in leaf litters strongly affected the rate of mass loss. He also suggested that decomposition was affected by other chemical factors. In oak leaves, HARRISON (1971) suggested that tannins affected the rate of mass loss.

In Scots pine needle litter, BERG & STAAF (1980) found that the nutrient level stimulated mass loss initially whereas in later decomposition stages the lignin level had a retarding effect that probably overtook the effect of nutrients. FOGEL & CROMACK (1977) found the lignin level to be more rate-determining than the C/N quotient or total nitrogen level.

Even if these factors — observed in needle litters — also influence mass loss rate for leaf litters there are additional influences on decomposition rate which are more pronounced for leaf than for needle litters. Thus, NYKVIST (1963) found that short-term leaching of whole leaves in water released considerable parts of their soluble material (about 10%) whereas only little organic substance was released from pine and spruce needles (<1%).

There are relatively few detailed long-term descriptions of leaf litter decomposition. Many of the studies have followed mass losses for one to two years, including leaching and nutrient release. LOUSIER & PARKINSON (1976) followed and described the decomposition kinetics for aspen and poplar leaf litter which was also followed with regard to ingrown fungal biomass (VISSER & PARKINSON 1973) and nutrient release (LOUISER & PARKINSON 1978). Another study concentrating on mass losses from sweet chestnut and beech leaf litter was carried out by ANDERSON (1973). Descriptions of organic-chemical changes during decomposition were carried out by SCHLESINGER & HASEY (1981) for chaparral shrub foliage and by TÖTH, PAPP & LENKEY (1973) for oak and maple leaves. In his laboratory study, MIKOLA (1954) compared decomposition of different common needle and leaf litters, including birch leaves, and also followed organic-chemical changes.

In an attempt to define a basic pattern for mass loss and chemical changes for birch leaf decomposition, a four-year incubation study was performed. For comparison, Scots pine needle litter was incubated simultaneously throughout most of the same period. Decomposition of Scots pine needles has been described in detail in another study carried out at this site. Birches often appear in Scots pine forests, especially in very young stands, after clear-cutting and forest fires. The description of the decomposition of birch leaves thus describes the process of an important litter component in the early stages in the development of a Scots pine system. At the present site, the soil animals present appear to have little effect on litter decomposition (BERG, LUNDKVIST, LOHM & WIRÉN 1980), a fact that provides us with a system with almost exclusively microbial decomposition of the litter.

The aim of the present paper is two-fold; one to describe the chemical changes of birch leaves during decomposition, the other to compare this with the decomposition of Scots pine needles.

## 2. Site description

The 120- to 130-year-old Scots pine stand studied is located at the SWECON research site, Ivantjärnsheden, Central Sweden (60° 49′ N, 16° 30′ E) at an altitude of 185 m on a flat area of deep glacifluvial sand sediments. The mean annual precipitation at a nearby village is 609 mm (1931—1960), and the mean annual temperature +3.8 °C. The length of the growing season is about 160 days. (Number of days with a daily temp. higher than 6 °C; AXELSSON & BRÅKENHIELM 1980.)

The tree layer is exclusively composed of *Pinus silvestris* L.[1]) and has a density of 393 trees $\mathrm{ha}^{-1}$ and a height of 17—19 m. *Calluna vulgaris* (L.) HULL. and *Vaccinium vitis-idaea* L. form a well-developed field layer, and the bottom layer, completely covering the ground, is mainly composed of the mosses *Pleurozium schreberi* (BRUD.) MITT. and *Dicranum polysetum* SV. together with *Cladonia* lichens. The most recent direct effect of forestry practices was a slight thinning in 1960. A more complete description is given by AXELSSON & BRÅKENHIELM (1980).

The soil profile is an iron podsol with a weakly developed bleached horizon (2—7 cm) and the humus type is a typical mor. A very loose litter layer ($A_{00}$), interwoven with living mosses and lichen, covers a humus layer ($A_{01}$—$A_{02}$) of 5—10 cm. The $A_{01}$ (F) and $A_{02}$ (H) horizons are almost indistinguishable from each other. The *p*H range is 3.9—4.2 in the humus layer and 4.6—4.8 in the upper mineral soil. The parent mineral material as well as the whole soil is considered to be very poor in essential nutrients. The C/N ratio of the $A_{01}$—$A_{02}$ layer is 42.3.

## 3. Materials and methods

### 3.1. Leaf and needle litter collection, storing and sample preparation

Leaves and needles were sampled at Ivantjärnsheden in September 1977 from the branches of about 15-year-old trees. The birch leaves were brownish-yellowish. Brown needles from the falling needle generation were taken at abscission from trees, all of which were located in an area less than $20 \times 50$ m². The needles were air-dried and then stored at —20 °C until the sample preparation took place.

Before weighing, the leaves and needles were air-dried at toom temperature to an even moisture level (about 5—8 %). Dry mass was determined at 85 °C and the largest difference in moisture was less than ± 0.5 % of the average (n = 20).

The litter-bags, made of terylene net with a mesh size of about 1 mm, measured $8 \times 8$ cm². An amount of about 0.7 g of either leaf or needle litter was enclosed in each bag.

### 3.2. Field incubations

Litter-bags were incubated in late October 1977 on the litter (L) layer in one measurement plot ($1 \times 1$ m²) in each of 20 blocks in a randomized block design in the 120-year-old Scots pine stand (3 ha). They were fastened to the ground by means of 10—15 cm long metal pegs stuck into the soil.

Samplings were made one to three times annually and on each occasion one sample from each of the 20 plots in the stand was collected. The litter-bags were transported directly to the laboratory where moss, lichen and ingrown dwarf shrub remains were removed. After drying at 85 °C the bags were weighed individually and then pooled to one sample for each set before chemical analyses and determination of fungal mycelium.

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[1]) There are no birches at the site but they represent a development stage of the forest and at a nearby site we have the species mixed. The site for litter collection had the very same soil type as the site where the decomposition experiment was carried out. The only difference is that it is younger and that it consequently was easier to collect litter there. We have also carried out chemical analysis on the pine litter from both sites and compared them. They are indistinguishable in our analysis.

### 3.3. Chemical analysis

The organic-chemical analyses were carried out according to the scheme presented by BERG, HANNUS, POPOFF & THEANDER (1982).

Samples were milled in a laboratory mill equipped with a filter allowing particles of less than 1 mm diameter to pass. The amount of water-soluble and ethanol-soluble substances were determined by sonicating the milled sample three times in a sonicator bath and weighing the samples after filtration and drying. The analyses for Klason lignin and solid carbohydrates (xylan, mannan, galactan, rhamnan, arabinan and cellulose) in the needle and leaf samples were carried out according to BETHGE *et al.* (1971).

Release of water-soluble substances from whole leaves and needles was investigated on separate samples by allowing the needles to soak in distilled water at room temperature for 10 and 24 h, respectively.

The milled samples were also analyzed for total contents of the elements N, P, K, Ca, Mg and Na. Double analysis was consistently used. Nitrogen was determined by a semi-micro Kjeldahl procedure (NIHLGÅRD 1972). After an acid wet oxidation in $HNO_3 + HClO_4$, analyses were performed for sulfur by a turbidometric analysis as $BaSO_4$-precipitate (BLANCHAR *et al.* 1965), for phosphorus by the vanadate yellow-complex method (JACKSON 1958) and for potassium by a flame photometric procedure. Calcium and magnesium were determined by atomic absorbtion spectrophotometry (Perkin-Elmer 403) in 1% LaCl-solution against acid standards (PAWLUK 1967). These analyses were carried out at the Department of Forest Ecology, Swedish University of Agricultural Sciences.

### 3.4. Determination of total fungal mycelium

Pooled samples of birch leaves and of Scots pine needles were milled to a particle size of $< 1$ mm. The milled samples were homogenized in an Ystral dispersion unit (1020) at 25,000 rpm for 5 min. Membrane filter preparations were made as described by HANSEN *et al.* (1974) and as modified by SUNDMAN & SIVELÄ (1978).

Observations and measurements were made with a Nikon apophot microscope using light-field illumination. Hyphal length was estimated by the intersection technique (OLSON 1950) at a magnification of ×500. One homogenate from each combined sample was studied, with four preparations per homogenate. Between 60 and 100 microscopic fields of view were counted. Biomass calculations were based on an average cross section of the hyphae of $9.3\,\mu m^2$, a density of $1.1\ g\ ml^{-1}$ and a dry mass of 15% (BERG & SÖDERSTRÖM 1979).

## 4. Results and discussion

### 4.1. Comments to the terminology

We have used the term "lignin" for those litter compounds which are not hydrolyzed in sulfuric acid according to the analysis method for sulfuric-acid lignin (BETHGE *et al.* 1971). The term is correct for the original litter material but not fully correct when used for decomposing litter since not only true lignin but also humification products are registered n the analysis (BERG, B., & O. THEANDER, unpubl.). We have preferred to use it, though, for the sake of simplicity.

The term "relative amount" has the same meaning as "concentration" whereas "absolute amount" is used to describe the changes in amounts.

We have used the term "solid part" for that part of the litter that was not soluble in water and ethanol *viz.* lignin and polymeric carbohydrates.

### 4.2. Initial chemical composition

#### *4.2.1. Organic-chemical components*

The pine and birch trees from which the litter was sampled had grown at the same site and it is thus reasonable to assume that the differences in composition could be ascribed to species rather than site effects as for example pine needles collected at this site differed little in chemical composition between years (STAAF & BERG 1981).

There were few large differences between birch leaves and pine needles in their dominant organic-chemical components. Nevertheless, the amounts of solubles were distinctly different. Whereas the needles contained only about 20% water-soluble substance the birch leaves had about 32%. The ethanol-soluble part, in magnitude equivalent to the amount of acetone solubles in these litters, made up 10 and 5%, respectively (Table 1). BERG *et al.*

Table 1. Relative amounts of organic chemical components in decomposing Birch *(B. pubescens)* leaf litter and Scots pine *(P. silvestris)* needle litter incubated in a 120-year-old Scots pine forest

| Date | Incubation time (days) | Mass loss (%) | Remaining amount (mg/g) | Solubles | | Solid components | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | in water (%) | in ethanol (%) | Lignin (%) | Cellulose (%) | Galactans (%) | Mannans (%) | Xylans (%) | Arabinans (%) | Rhamnans (%) |
| **Birch leaves** | | | | | | | | | | | | |
| 77-10-27 | 0 | 0.0 (—) | 1,000.0 | 32.1 | 5.6 | 26.3 (42.2)[1] | 16.4 (26.3)[1] | 4.1 (6.6)[1] | 1.1 (1.8)[1] | 7.5 (12.0)[1] | 4.7 (7.5)[1] | 2.3 (3.7)[1] |
| 78-05-22 | 208 | 34.2 (1.51) | 657.7 | 5.7 | 4.9 | 46.0 | 20.0 | 4.3 | 1.4 | 11.8 | 4.8 | 1.1 |
| 78-08-31 | 309 | 40.0 (0.56) | 600.0 | 4.0 | 4.3 | 48.0 | 20.2 | 5.8 | 2.5 | 9.0 | 4.8 | 1.5 |
| 78-10-16 | 355 (1 yr) | 43.0 (0.69) | 569.8 | 4.1 | 3.7 | 48.2 | 21.1 | 5.1 | 3.0 | 8.5 | 4.5 | 1.9 |
| 79-05-30 | 581 | 44.0 (1.00) | 560.2 | 3.6 | 2.5 | 51.2 | 20.4 | 5.3 | 2.2 | 8.3 | 5.1 | 1.6 |
| 79-08-30 | 673 | 48.0 (1.30) | 520.0 | 5.1 | 1.9 | 49.8 | 22.0 | 5.1 | 2.5 | 7.5 | 4.4 | 1.8 |
| 79-11-07 | 742 (2 yrs) | 51.2 (1.63) | 487.7 | 3.5 | 3.3 | 49.5 | 20.5 | 6.0 | 3.4 | 7.2 | 4.8 | 1.7 |
| 80-05-21 | 937 | 56.1 (1.13) | 439.0 | 5.3 | 3.7 | 50.2 | 20.4 | 4.1 | 2.5 | 6.5 | 4.9 | 2.2 |
| 80-09-01 | 1,040 | 60.2 (1.71) | 398.3 | 4.5 | 4.8 | 50.0 | 21.4 | 4.3 | 2.2 | 6.1 | 4.5 | 2.2 |
| 80-10-30 | 1,100 (3 yrs) | 63.0 (2.06) | 369.8 | 3.7 | 4.0 | 50.8 | 21.4 | 4.4 | 2.5 | 6.6 | 4.4 | 2.5 |
| 81-05-23 | 1,304 | 63.8 (1.74) | 361.9 | 3.9 | 2.5 | 50.6 | 22.2 | 4.1 | 2.2 | 6.9 | 4.3 | 1.7 |
| 81-10-26 | 1,461 (4 yrs) | 65.4 (1.82) | 346.3 | 4.0 | 3.5 | 50.6 | 21.6 | 4.0 | 2.1 | 6.7 | 4.2 | 1.7 |
| **Scots pine needles** | | | | | | | | | | | | |
| 77-10-27 | 0 | 0.0 (—) | 1,000.0 | 20.2 | 10.2 | 22.3 (32.0)[1] | 29.1 (41.8)[1] | 3.2 (4.6)[1] | 8.0 (11.5)[1] | 2.6 (3.7)[1] | 3.9 (5.6)[1] | 0.6 (0.9)[1] |
| 78-05-22 | 208 | 17.7 (0.34) | 823.5 | 6.2 | 9.1 | 32.8 | 32.9 | 3.5 | 9.0 | 3.0 | 2.9 | 0.7 |
| 78-08-31 | 309 | 25.9 (0.42) | 740.8 | 5.2 | 8.2 | 34.8 | 32.8 | 3.6 | 8.9 | 3.0 | 2.7 | 0.7 |
| 78-10-16 | 355 (1 yr) | 31.1 (0.57) | 689.0 | 4.6 | 7.6 | 36.2 | 32.8 | 3.3 | 9.5 | 3.0 | 2.4 | 0.6 |
| 79-11-07 | 742 (2 yrs) | 53.0 (1.43) | 469.6 | 4.2 | 9.8 | 37.1 | 32.1 | 3.4 | 7.8 | 2.5 | 2.6 | 0.7 |
| 80-10-30 | 1,095 (3 yrs) | 65.1 (1.36) | 349.1 | 4.8 | 10.1 | 44.1 | 28.3 | 2.5 | 5.1 | 1.7 | 2.5 | 0.9 |

[1] Calculated as percentage of the solid components.

Standard error within parenthesis. The analysis scheme given by Berg *et al.* (1982) was used also here.

Table 2. Decomposition of birch *(B. pubescens)* leaf litter and Scots pine *(P. silvestris)* needle litter in different time periods

| Birch | | | | | | | | Scots pine | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| period (days) | mass loss (%) | | chemical components (mg · g$^{-1}$) | | | | | mass loss (%) | | chemical components (mg · g$^{-1}$) | | | | |
| | accumulated | period | N | P | S | solubles | lignin | accumulated | period | N | P | S | solubles | lignin |
| 0—208 | 34.2 | 34.2 | 7.6 | 2.4 | 0.46 | 377 | 263 | 17.7 | 17.7 | 4.1 | 0.19 | 0.38 | 304 | 223 |
| 208—309 | 40.0 | 8.8 | 11.0 | 0.81 | n.d. | 106 | 460 | 25.9 | 10.0 | 5.6 | 0.32 | n.d. | 153 | 328 |
| 309—355 | 43.0 | 5.0 | 12.5 | 1.00 | n.d. | 83 | 480 | 31.1 | 7.0 | 5.8 | 0.37 | n.d. | 134 | 348 |
| (years) | | | | | | | | | | | | | | |
| 0—1 | 43.0 | 34.2 | 7.6 | 2.4 | 0.46 | 377 | 263 | 31.1 | 17.7 | 4.1 | 0.19 | 0.38 | 304 | 223 |
| 1—2 | 51.2 | 14.4 | 13.3 | 0.96 | n.d. | 78 | 482 | 53.0 | 31.8 | 6.0 | 0.36 | n.d. | 122 | 362 |
| 2—3 | 63.0 | 24.2 | 17.1 | 1.10 | n.d. | 68 | 495 | 65.1 | 25.7 | 7.8 | 0.52 | n.d. | 140 | 371 |
| 3—4 | 65.4 | 6.4 | 17.7 | 1.04 | n.d. | 37 | 508 | — | — | — | — | — | — | — |

Note: Concentrations of chemical components are given for the start of each period. Rate constants calculated from the accumulated mass loss with mass loss values for 1, 2 and 3 years (cf. Olson 1963) were 0.352 and 0.311 for the birch leaves and pine needles respectively. n.d. not determined.

(1980) studied in detail the composition of the soluble part of Scots pine needles but such a study does not appear to exist for birch leaves. It is possible, though, that pine needles may contain a higher level of soluble phenolic substances, an observation supported by the measurements of BOGATYREV *et al.* (1983) carried out on litter from this site.

Of the solid components, the glucans dominated in the needles with 29% whereas the leaves had only about 16%. The other polymeric carbohydrates varied also to some extent. Thus, the level of xylans was about 7% in the birch leaves compared with 2—3% in the needles. The concentrations of arabinans and galactans were about 4% in both litter types. Differences could be seen in the mannans fraction, which were 1 and 8%, and in the concentrations of sulfuric acid lignin with about 26 and 22% in leaves and needles respectively (STAAF & BERG 1981) the levels in the needles were found to vary little between years — the variation in, for example, the sulfuric-acid lignin fraction being 19—25%.

### *4.2.2. Inorganic-chemical composition*

The levels of different nutrients were generally higher in the birch leaves. Thus, the nitrogen level was almost double that in needle litter, with 7.6 and 4.1 mg $g^{-1}$ respectively, whereas the sulfur levels were alike (0.4 mg $g^{-1}$). A drastic difference was noted in phosphorus levels, with the leaves having a concentration 10 times that in the needles (2.4 *vs* 0.19 mg $g^{-1}$). This value appears extreme compared to those reported by AARNIO (1935) and VIRO (1955). We may note, though, that due to our material being shaken from the trees, very little was leached from our litter before the sampling took place. Similar differences were found for magnesium and potassium, with 2.8 and 0.42 mg $g^{-1}$ and 4.3 *vs* 0.87 mg $g^{-1}$, respectively. For calcium and manganese the concentrations were twice as high in birch leaves as in needles (11.5 *vs* 6.0 and 2.6 *vs* 1.0 mg $g^{-1}$, respectively).

### *4.2.3. Mass loss of litter*

In the first winter there was a heavy mass loss from the birch leaves (34%) whereas the needle litter was degraded by only 18% (Fig. 1). The heavy mass losses from birch leaves were probably largely due to leaching (see next section).

After one year's incubation the difference in mass loss was less pronounced, with 43 and 31% respectively, but still significantly higher for leaves. After two years the accumulated mass loss was higher for the needle litter with 53%, compared with 51 for the leaves (Fig. 1). After three years this difference still persisted (65 and 63%, respectively). MIKOLA (1954) also observed in laboratory experiments that several tree litters — among them birch leaves and pine needles — had reached similar accumulated mass losses after 300 days' incubation, *viz.* around 50% decomposition.

When regarding the separate periods and the decomposition taking place in these periods we can see that in the first 208 days the leaves lost mass to 34.2% and the needles 17.7%. In the periods between 208 and 309 days and between 309 and 355 days the mass loss was somewhat higher for needle litter. During the second year (365—742 days) the decomposition was 14.4 and 31.8% respectively for leaves and needles and during the third year 24.2 and 25.7% (Table 2).

The decomposition of whole litter followed a first order kinetics (OLSON 1963) fairly well (Table 2) both for the leaves ($p < 0.05$) and for the needles ($p < 0.001$) as calculated from all the measurements. To be able to compare the magnitude of the rate constants for the two litter types we calculated $k$ from the common measurement points and we used those for 1, 2 and 3 years' incubation. The rate constant thus calculated was higher for needle litter ($k = 0.352$) than for leaf litter ($k = 0.311$). However, the rate constants were not significantly different for the two litter types.

### *4.2.4. Mass loss of organic-chemical components*

In the first winter the water soluble fraction decreased from 32% for birch leaves and 20% for pine needles respectively down to fairly steady levels of about 4—6% (Table 1).

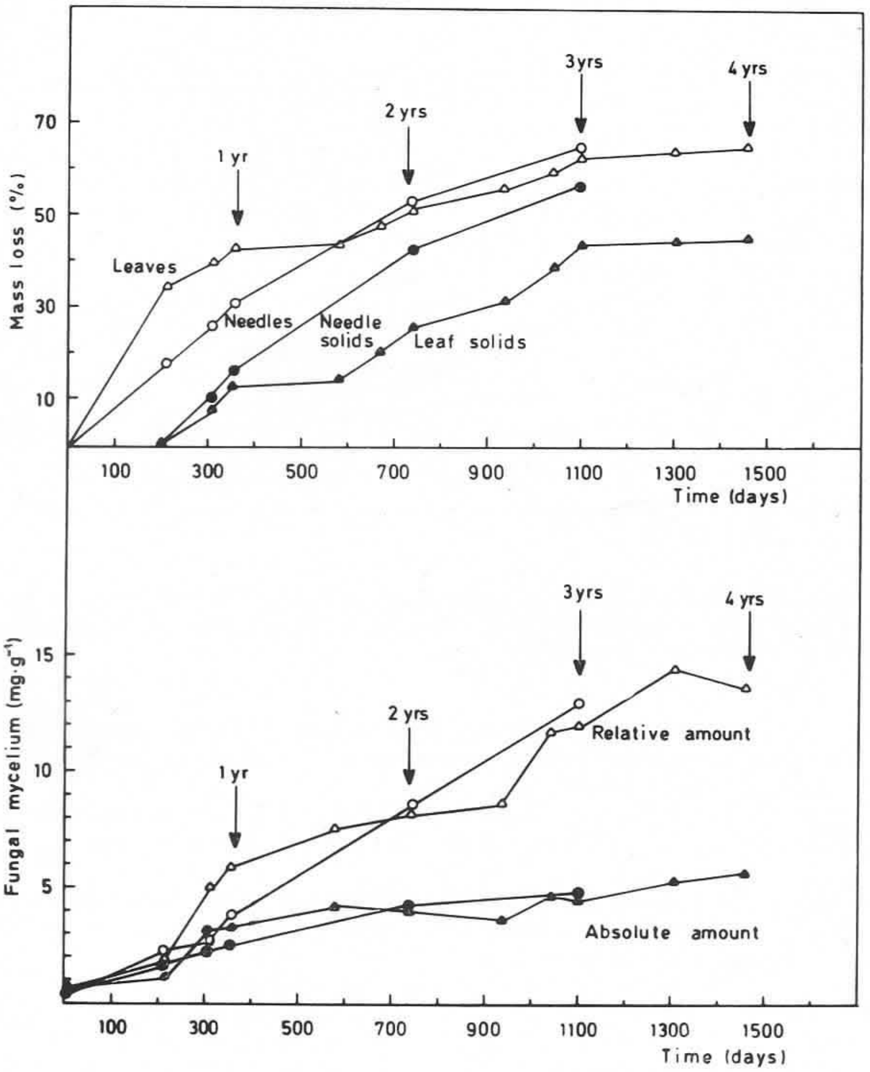


Fig. 1. Mass loss of Scots pine *(P. silvestris)* needle litter as compared to that of birch *(Betula pubescens)* leaf litter and the development of fungal mycelium in the 4-year incubation period. Upper part; mass loss of (△) whole birch leaves, (○) whole needles, (▲) solid part of birch leaves, (●) solid part of Scots pine needles. Lower part; development of fungal mycelium, (△) relative amount in birch leaves, (○) relative amount in needles, (▲) absolute amount in birch leaves, (●) absolute amount in needles.

Part of the soluble substance was probably leached from the birch leaves but part of it was degraded microbially within the leaves. This is supported by the observation that these leaves lost 12% of their mass in leaching experiments in the laboratory. The needles lost about 1%. Both these results were close to the values found by NYKVIST (1963). A further support may be the observation that the ingrown fungal biomass after the first winter was similar in magnitude in both pine needles and in the leaves. As the solubles in needles were leached to a very low extent, they consequently were degraded almost exclusively within the needles. The disappearance of the solubles as an analytical fraction was fast in this experiment (Fig. 2). For pine needles it is seen (BERG *et al.* 1982) that different

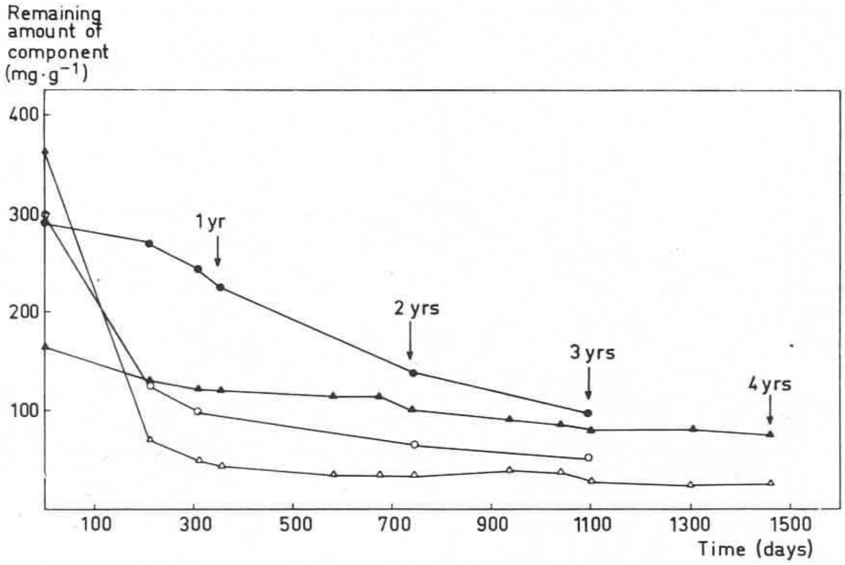


Fig. 2. Remaining absolute amounts of solubles and cellulose from initially 1,000 mg birch leaf and pine needle litter. (△) solubles in birch leaves, (▲) cellulose in birch leaves, (○) solubles in pine needles, (●) cellulose in pine needles.

soluble components were degraded at very different rates. Here, the ethanol-soluble part and a lower disappearance rate in both needles and leaves and its concentration in needles remained fairly constant for three years.

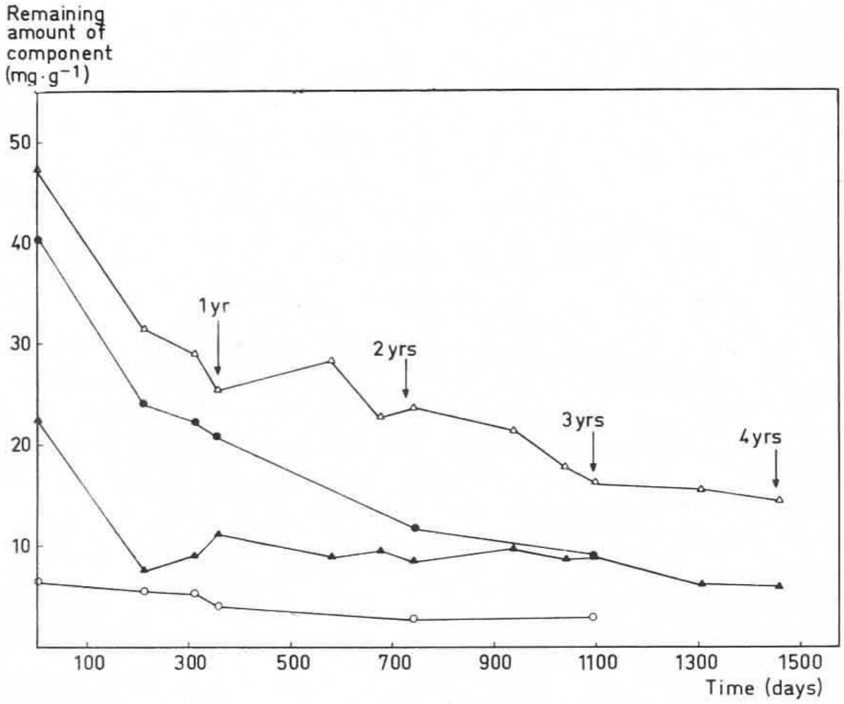
The solid part (*viz.* lignin and polymer carbohydrates) of the pine needles was degraded at a significantly higher rate than was the solid part of the birch leaves ($p < 0.001$; $R^2 = 0.986$).

The various polymer carbohydrates behaved differently in the decomposition process. In both litter types some had an initially high decomposition rate which later slowed down, whereas others had a more constant rate.

The glucans (cellulose) fraction of the pine needles was degraded faster than that of the birch leaves (Fig. 2) *viz.* 66 % and 52 % respectively in three years. The relative amounts increased in both cases (Table 1). The xylans of pine needles were decomposed by 78 % in three years, whereas those of birch leaves were degraded by 67 % (Fig. 3). The mannans of the pine needles were degraded by 78 % in three years whereas in birch leaves an absolute increase of about 50 % seemed to take place in the first year (Fig. 3). In three years' time a very small decrease may have taken place, though. The increase in absolute amount went from initially 10 mg up to 15 mg after one year and after a minor decrease a new peak was reached after two years. Both peaks were reached in late autumn. These increases could be due to ingrown fungal mycelium as many fungal species contain mannans (*cf.* Fig. 1). However, the amount of mycelium measured is of such an order of magnitude that it could only partly explain the pattern.

The galactans showed a behaviour fairly similar to that of mannans and were degraded by 72 and 60 % respectively for needles and leaves in three years (Fig. 3). For both litter types (birch and pine) the arabinans were degraded relatively rapidly in the first year, by 45 and 48 %, respectively, which also was found by BERG *et al.* (1982). In three years they were degraded by 66 and 78 % respectively (Fig. 3). The small fraction of rhamnans seemed to be degraded fairly slowly.

The concentration of sulfuric-acid lignin increased in both litter types as decomposition proceeded (*cf.* BERG *et al.* 1982). For birch leaves a steady level was reached at about 50 %



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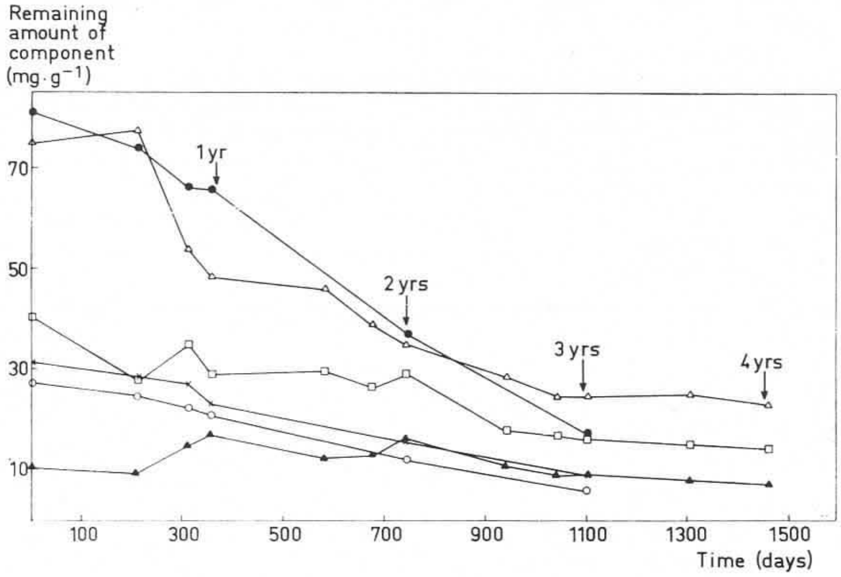

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Fig. 3. Changes in absolute amounts of some organic-chemical components from initially 1,000 mg decomposing birch leaves and Scots pine needle litter. A. Birch leaves (△) xylans, (▲) mannans, (□) galactans. Pine needles (○) xylans, (●) mannans, (×) galactans. B. Birch leaves (△) arabinans, (○) rhamnans. Pine needles (●) arabinans, (▲) rhamnans.

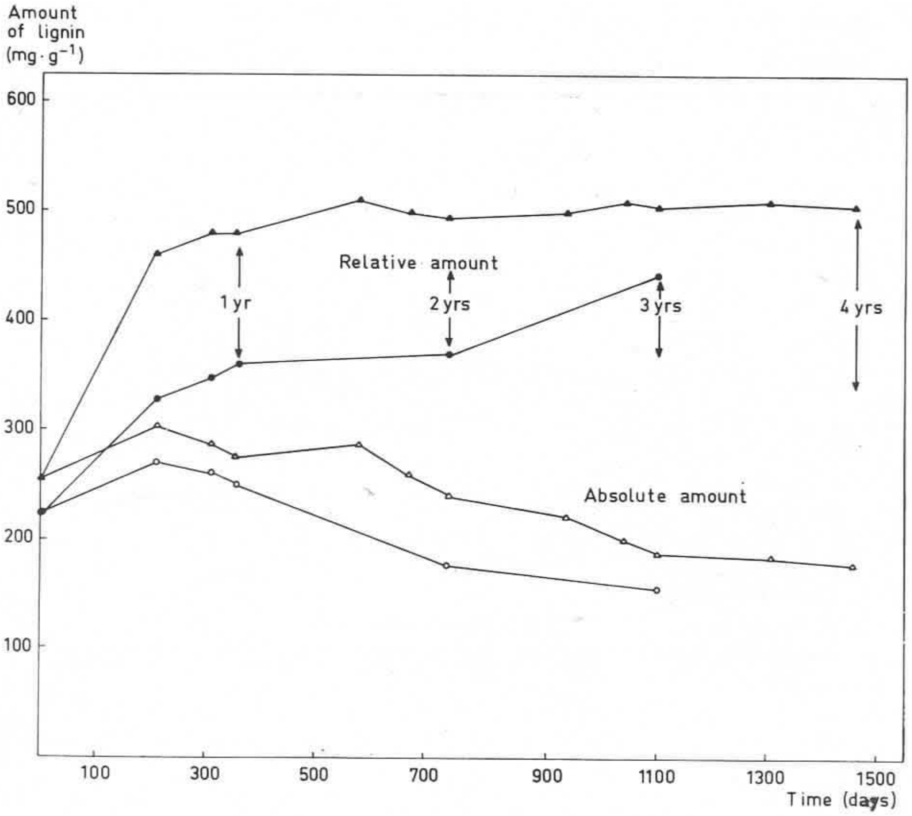

Fig. 4. Mass loss from and relative changes in the sulfuric-acid lignin fraction in decomposing birch leaves and Scots pine needle litter. Change in absolute amount of lignin from initially 1,000 mg litter. (△) birch leaves, (○) pine needles. Relative changes in % (▲) birch leaves, (●) Scots pine needles.

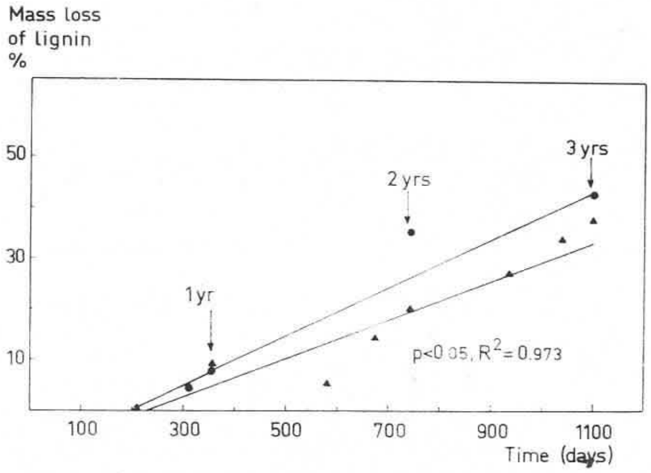

Fig. 5. Decomposition of sulfuric-acid lignin as calculated from the moment when the decomposition started. (▲) birch leaf lignin, (●) Scots pine needle lignin.

after one year's incubation (Fig. 3; Table 1) whereas for needle litter this relative increase was slower and reached 44 % after three years. In a similar set of needle litter BERG *et al.* (1982) found this increase to continue for about five years up to 47 % — a level that was reached at about 60 % mass loss.

The absolute amount of lignin increased in the early stages — probably due to humification (BERG, B., & THEANDER, unpublished) but after about 200 days the decomposition started and was fairly slow (Fig. 4) with about 13 % per year for the birch leaf lignin and about 20 % per year for the needle lignin. The rate of lignin decomposition over three years was significantly higher for the needle lignin than for that of birch leaves ($p < 0.05$; $R^2 = 0.973$; Fig. 5).

### 4.2.5. *Ingrowth of mycelium*

Both litter types had initially very similar amounts of mycelium (0.5 mg $g^{-1}$), probably from the surface of the live leaves. The new colonization that took place in the first winter in the forest floor was low both relatively and absolutely. For both litters the ingrown absolute amount was similar — possibly lower for the birch leaves. This supports the idea that much of the water-soluble material was leached in this period instead of supporting mycelium growth. Apparently the higher nutrient level in birch leaves had little effect on growth. From May until October there was a marked increase of mycelium in the leaves, *viz.* a relative increase from 1.8 to 5.9 mg $g^{-1}$, while in the needles only a low increase took place (2.1 to 3.8 mg $g^{-1}$). The difference in absolute amounts was less marked but nevertheless the same tendency was seen. The increased temperature in the spring/summer period was necessary for fast growth and temperature appeared to be more limiting in the first winter than, e.g., the nutrient level.

In the second year the relative amount of mycelium in needles increased more than that in leaves and it appears that the concentrations were no more different. The higher amount indicated in the figure was not significant.

In both cases the relative amounts of mycelium increased with time (to about 13 mg $g^{-1}$) after three years' incubation ($> 60$ % mass loss) and thus there was no real difference between the two litter types in this respect (Fig. 1). There were linear relations between mass loss and relative amount with $p < 0.001$ and $p < 0.001$ for the two litter types. When this linear relation is extrapolated we may calculate that at 90 % mass loss there will be about 2 % fungal biomass.

Humus originating from decomposing birch leaves is often considered to be of a mull type, whereas that originating from pine litter gives a mor. In the latter type more fungal mycelium is found (SWIFT *et al.* 1979). Such a characteristic was not seen in the litter of the present investigation where the levels of total mycelium were similar in both litter types when decomposition had proceeded to above 50 % mass loss.

### 4.2.6. *Factors regulating mass loss of the litters*

The relatively high initial mass loss of leaf litter, could be attributed both to decomposition and leaching of the soluble part.

With regard to the solid part of the litter which started to decompose in spring — after about 208 days of incubation — it appears that the decomposition was not positively correlated to nutrient level. On the contrary, the solid part of the needle litter was degraded faster than that of birch leaves and when approximated to linear functions this difference was significant ($R^2 = 0.99$; $p < 0.001$). The decomposition of the lignin fraction (Fig. 4) started at about 200 days of incubation and the mass loss of the birch leaf lignin was found to be significantly slower ($R^2 = 0.973$; $p < 0.05$) than that of pine needles. Considering the unspecific analysis method used for lignin we may not exclude the possibility that humic substances were synthesized faster in the birch leaf litter than in needles.

It is reasonable to compare this difference in rate to that obtained for lignin in the Scots pine needles investigated by BERG, WESSÉN & EKBOHM (1982). They found a significantly

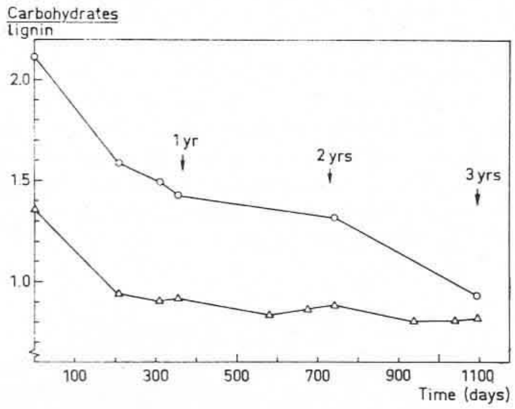

Fig. 6. Changes in the carbohydrate: lignin ratio of the solid part of birch leaves (△) and Scots pine needles (○) during decomposition.

lower decomposition rate for lignin in needles with a higher nitrogen level (initially about 1.2% *vs* 0.4%) and speculated in two different explanations for the effect of nitrogen as a rate-retarding agent.

In the light of a finding by Kirk *et al.* (1976) we also must consider the availability of the carbon source. They found that two lignin-degrading fungi needed another carbon source, such as cellulose, to be able to degrade lignin. They also clearly demonstrated — in laboratory cultures — that progressively increased amounts of cellulose, *viz.* higher carbohydrate: lignin ratios, increased the decomposition rate for lignin. The ratio between the sum of solid carbohydrates and lignin for birch leaves and the pine needles (Fig. 6) shows that there were relatively more carbohydrates in the latter when lignin degradation started (1.6. compared to 0.95 for birch leaves) at about 208 days. The pine needles had then about 40% more carbohydrate — a difference, which after two years' incubation, was about 30% and after three years about 10%. When Kirk *et al.* (1976) changed the ratio between cellulose and lignin from 0.1 to 1.0 in their laboratory cultures they obtained a 12-fold increase in decomposition rate for lignin.

## 5. Concluding remarks

When growing on the very same mor soil, birch *(Betula pubescens)* sheds a more nutrient-rich litter than Scots pine. The amounts of leaf and needle litter shed in the autumn may be of similar magnitude in birch and pine forests (Viro 1955; Mork 1946), *viz.* about 100 g $m^{-2}$ $year^{-1}$, and we may thus conclude that the birch actively transports up to the S- and L-layers a considerably larger amount of essential nutrients. The higher *p*H, together with the large amount of phosphorus, probably in addition causes a strong increase in nitrogen fixation among the non-symbiotic nitrogen fixers.

Both nitrogen and phosphorus appear to be limiting for organic matter turnover in Scots pine systems (Berg & Staaf 1980; Staaf & Berg 1982), and the apparently stronger transport in birch forests may thus cause a higher soil activity in such systems as compared to pine forests which also can be expected in a mixed birch — pine forest. The amount of leached organic material probably will be of a magnitude of 15—20 g $m^{-2}$. The material has, of course, a complex chemical composition but may be expected mainly to stimulate the soil microflora.

The decomposition constants may be used to calculate the amounts of accumulated organic material (Olson 1963) from leaf and needle litter. In such an example, calculating over 50 years and assuming 100 g of litter each year, we obtained a higher accumulation in a hypothetical birch forest (about 10% more). If we use rate constants for the solid material only, which follows a first order kinetics better than whole litter ($p < 0.001$), the difference becomes more apparent. This example is limited, though, to nutrient-poor mor soils similar to those at the site where the work was carried out. We cannot, of course exclude the possibility that the observed effects are limited to sites dominated by pines and that the microbial population in a birch forest may cause another decomposition pattern. As the levels of N, P and S tend to increase linearly with mass losses it is possible that the organic material accumulated, apart from increasing the amount, would also make the humus richer in at least some essential nutrients.

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Berg, B., & B. Wessén, 1984. Changes in organic-chemical components and ingrowth of fungal mycelium in decomposing birch leaf litter as compared to pine needles. Pedobiologia **26**, 285—298.

The organic-chemical changes were studied for decomposing birch leaf litter and related to those of Scots pine needle litter, earlier studied in detail at this site. Birch leaves had higher concentrations of water soluble substances, lower levels of glucans but higher concentrations of mannans and xylans, whereas lignin levels were fairly similar. Birch leaves also had higher concentrations of the major nutrients, N, P and S.

The leaves lost mass faster in the first year but already after two years needle litter was degraded to a higher extent — a tendency that prevailed. The decomposition of the lignin fraction of the birch leaves took place at a significantly lower rate from the beginning, though, as did the whole solid part. Possible rate-regulating factors are discussed.

The relative amount of fungal mycelium was higher in birch leaves in the first year. The absolute amount was similar for both litter types during the three years of comparison.

**Key words:** Birch litter, needle litter, decomposition, mass loss, litter-bag, fungal mycelium, lignin, cellulose.

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